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Short communication

Seasonal variation in the reproductive activity and biochemical composition of the Pacific oyster (*Crassostrea gigas*) from the Marlborough Sounds, New Zealand

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Abstract Reproductive cycles of the Pacific oyster *Crassostrea gigas* (Thunberg) from the Marlborough Sounds, New Zealand, were followed between June 1998 and January 2000. Histological examination of the gonad confirms an annual cycle with a winter inactive period followed by rapid gonad development and a single short spawning period. The population gonad index correlated with seawater temperature and changes in tissue dry weight, condition index, and biochemical components. In winter, few individuals with early gametogenic stages were present and rapid development of primary oocytes (diam. 11 µm) occurred during spring (September–November). The developmental rate and the diameter of mature oocytes (37 µm) was similar for the 1998 and 1999 seasons. For a standard 110-mm-length oyster, maximal tissue body weight and condition index were recorded in December. Rapid weight loss in January was length dependent and was attributed to spawning. Temperature was the environmental variable which best correlated with the timing of gametogenesis. Food availability (phytoplankton biomass) may have been responsible for inter-annual variations. The biochemical composition (% glycogen, lipid, protein) of separated gonad and somatic tissues were variable seasonally and annually. Gametogenesis (oocyte diameter) was associated with increased gonad protein and glycogen and a decrease in lipid concentrations. These changes are similar to those in Pacific oyster populations from other parts of the world.

Keywords oyster; *Crassostrea gigas*; gametogenesis; reproductive cycle; biochemical composition

INTRODUCTION

The Pacific oyster *Crassostrea gigas* (Thunberg) was introduced accidentally into New Zealand in the 1960s and spread rapidly over the next 10 years into many estuaries in the North Island (Dinamani 1978). It is now established in the northern part of the South Island, the Marlborough Sounds and the Nelson region. The Pacific oyster is commercially cultured worldwide and there have been numerous studies on its reproductive cycle and biochemical composition (Perdue et al. 1981; Whyte & Englar 1982; Héral & Deslous-Paoli 1983; Whyte et al. 1990; Robinson 1992; Ruiz et al. 1992; Robert et al. 1993; Park et al. 1999; Kang et al. 2000). These studies suggest that seasonal variations in oyster production result from the storage and allocation of metabolic reserves into growth and reproduction. However, many internal and environmental factors including pollutants can affect the growth and reproductive success of marine bivalves (MacDonald & Thompson 1985; Steele & Mulcahy 1999) and recent studies suggest complex interactions of temperature, food quality, and quantity (Berthelin et al. 2000a; Seguineau et al. 2001).

In New Zealand, Dinamani (1987) described the gametogenic patterns of *C. gigas* from Northland but

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did not evaluate the biochemical components. These can provide evidence of nutrient storage and energy allocation and thus affect meat production within culture systems (Ruiz et al. 1992; Paniagua-Chávez & Acosta-Ruiz 1995). This research characterised the gametogenic cycle of Pacific oysters from the Marlborough Sounds, in an area thought to be close to the southern limit of this species. We investigated the seasonal relationships between gametogenesis, biochemical composition, and environmental factors in *C. gigas* and the results provide basic parameters for a dynamic energy budget model (Ren & Ross 2001) to assess oyster culture success in different parts of New Zealand.

MATERIALS AND METHODS

Oyster collection and sample preparation

Oysters, *C. gigas*, were collected from Croiselles Harbour, Marlborough Sounds, on the north coast of the South Island of New Zealand (173°42′–46′E, 41°02′–05′S). This is an area of intensive suspended rope culture of the oyster and the mussel (*Perna canaliculus*). Over 60 oysters were collected at bi-weekly–monthly intervals from a single oyster farm from 19 June 1998 to 18 January 2000. They were transported live to the laboratory for biochemical, reproductive, and weight determinations. Fouling organisms were carefully removed from the shell surface using a scalpel. Body tissue from 15 to 20 oysters (length 110 ± 10 mm) was separated into gonad tissue from the mantle and remaining somatic tissue. These were dried on aluminium foil at 60°C for 72 h to constant weight. The shell valves were also dried at 60°C for 72 h and weighed for determination of the dry weight condition index.

Additional samples of oysters 50–150 mm shell length were collected in December 1998, 1999 (n = 56), and January 1999 and 2000 (n = 36). These individuals were used to compare the dry tissue weight and length relationships just before and during the predicted spawning period. These were used to estimate the reproductive output (Bayne & Worrall 1980; Heffernan et al. 1989; Harvey et al. 1993).

Environmental measurements

Surface water temperature and phytoplankton cell counts were provided by the Marlborough Sounds Shellfish Quality Programme. Four replicate temperature measurements were taken at intervals that varied from 1 to 4 weeks. At weekly intervals, a 250 ml sample of seawater was collected 2 m below the surface to assess phytoplankton abundance. This was preserved immediately in Lugol's iodine. The phytoplankton sample was allowed to settle in the laboratory and decanted to 25 ml, then placed in a settling chamber for a further 24 h. The phytoplankton cells were identified and counted by staff at the Cawthron Institute using a Wild inverted microscope as described by Utermohl (1958). Because phytoplankton cells differ in size, nutritional value, and composition seasonally, total cell density may not reflect the nutritional value. The phytoplankton densities were therefore converted into organic carbon values (mg litre^{-1}) according to cell size and taxonomic group (Strathman 1967; Eppley et al. 1970). The organic carbon values more accurately reflect the nutritional value of the plankton over time than phytoplankton density and the results can be compared with studies elsewhere (Hummel 1985).

Biochemical analysis

The biochemical analyses were done on tissue samples from individual oysters. Tissues from 3–6 oysters from each monthly sample were separated into mantle tissue containing gonad tissue and the remaining somatic tissue. They were freeze dried (Giese et al. 1967; Barnes & Blackstock 1973) then ground into a powder with a mortar and pestle for biochemical analyses.

Total protein was estimated from a known amount of freeze-dried tissue using a modification of the Kjeldahl method where digestion of the dry powder was followed by phenol-hypochlorite determination of ammonia (Holland & Hannant 1973). A sample of 15 mg was catalytically digested with sulphuric acid, converting the total organic nitrogen into ammoniac nitrogen. The ammonia is released by the addition of sodium hydroxide, absorbed in boric acid, and then titrated with HCl. The protein content was estimated from the nitrogen content multiplied by 6.25 (Thompson 1984).

Lipid concentrations were determined using the gravimetric method of Barnes & Blackstock (1973). The assay used 500 mg of the dried sample homogenised in 5 ml of double-distilled water and left overnight in the fridge (5°C). For the gravimetric assay of lipids, aliquots of the homogenate were extracted in 5 ml of 2:1 v/v chloroform:methanol (Folch et al. 1957). Lipid residues were weighed using a Mettler AE200-S microbalance, after evaporation of the chloroform using liquid nitrogen.

Glycogen was determined using the method of Hewitt (1958). A sample of 100 mg powder was

homogenised in sulphuric acid reagent to make 5 ml homogenate solution and extracted overnight at 5°C. The homogenate solution was thoroughly vortex mixed before being centrifuged and subdivided into two portions. While one portion was incubated in a water bath at 95°C for 4 h, the other was stored at 5°C. The optical density of both portions was determined at 340 nm using a spectrophotometer (Kontron UVIKON 860). A calibration curve using D-glucose as a standard was determined.

Reproduction

Ten oysters, collected at approximately monthly intervals from 31 July 1998 to 18 January 2000 were used for histological examination. Reproductive tissue (5× 5 × 5 mm) was dissected from the oyster gonad contained within the mantle. This was fixed in Baker's formol calcium fixative with 2.5% sodium chloride for 24 h. The oyster tissues were placed in cassettes for processing and embedded in paraffin wax. Sections of 7 µm thickness were cut using a microtome (Leica RM2165) and mounted on glass slides. The sections were stained with hematoxylin and eosin (Luna 1968). The stained slides were rendered semi-permanent using a mounting medium and coverslips.

Five gametogenic stages and their frequency of occurrence were recorded, based on the classification of Dinamani (1987): 0 = inactive/spent follicles; 1 = early active; 2 = late active follicles; 3 = mature gametes; 4 = fully ripe/spawning phase. The gonad index was the mean value calculated for each seasonal sample.

Oocyte diameter was estimated from ovary sections using a microscope (Leica MPS 60). Since oocytes deviate strongly from a spherical shape, measurements were made of the longest and shortest axes of c. 50 oocytes and each pair of measurements were added and then divided by two.

Mature oysters lose a large proportion of their body weight during spawning (Brown & Russell-Hunter 1978; Park et al. 1999) and the reproductive output was calculated as a difference in dry tissue weight before and after spawning. There is strong evidence that reproductive effort increases with size or age in marine bivalves (Griffiths & King 1979; Bayne & Worrall 1980; Griffiths 1981; Thompson 1984). The weight relationships were therefore described by an allometric function of length as:

$$DTW = aL^b$$

where DTW is dry tissue weight (g), L is length (cm), a is the coefficient, and b is the exponent.

RESULTS

Environmental variables

Surface water temperatures recorded in Croiselles Harbour during the study (Fig. 1A) were highest during January–February and the lowest during July–August with little variation between years. Intra-annual and inter-annual variation occurred in phytoplankton biomass (Fig. 1B). In 1998, high values for carbon biomass were recorded in June and August (winter) but for the rest of the year the phytoplankton biomass was generally low (average = 4.95 mg C litre^{-1}). In 1999, the phytoplankton biomass was generally higher throughout the year with peaks during January and February (average = 8.58 mg C litre^{-1}). At each time interval there was no direct correlation between temperature and carbon biomass, however carbon biomass followed the temperature values with an approximate delay of a month (correlation coefficient 0.43, n =19, $P <$ 0.05).

Gametogenesis

Gonad development in *C. gigas* follows an annual cycle (Fig. 2A,B) with peak activity over summer (November–January) and relative inactivity from April to August. There was temporal variability in the proportions of male, female, and undifferentiated oysters with females dominating the samples. Relatively few early development stages of both male and female oyster gonad were discernible over winter when the gonad index was <1. Early gametogenesis was characterised by an oocyte diameter close to 11 µm in both the 1998 and 1999 seasons and development proceeded quite rapidly during the spring to an average close to 37 µm in December of both years (Fig. 3). The oocyte development rate was similar in both 1998 and 1999 (analysis of covariance, $P > 0.69$). Although the sections showed little direct evidence of spawning, this most likely occurred in January in both years of the study with some oysters showing evidence of oocyte reabsorption and re-differentiation into small primary oocytes. Oocyte diameter was directly related to surface seawater temperature (linear regression analysis R^2 = 0.93) and the mean gonad index (Fig. 4, Table 1). Although these results suggest a limited spawning period, the presence of late stage male and female gametes over much of the spring and summer suggest that spawning could occur in some individuals from September. However, the peak in gonad maturity occurred in November and from March there was gamete degeneration and resorption. In April, oyster

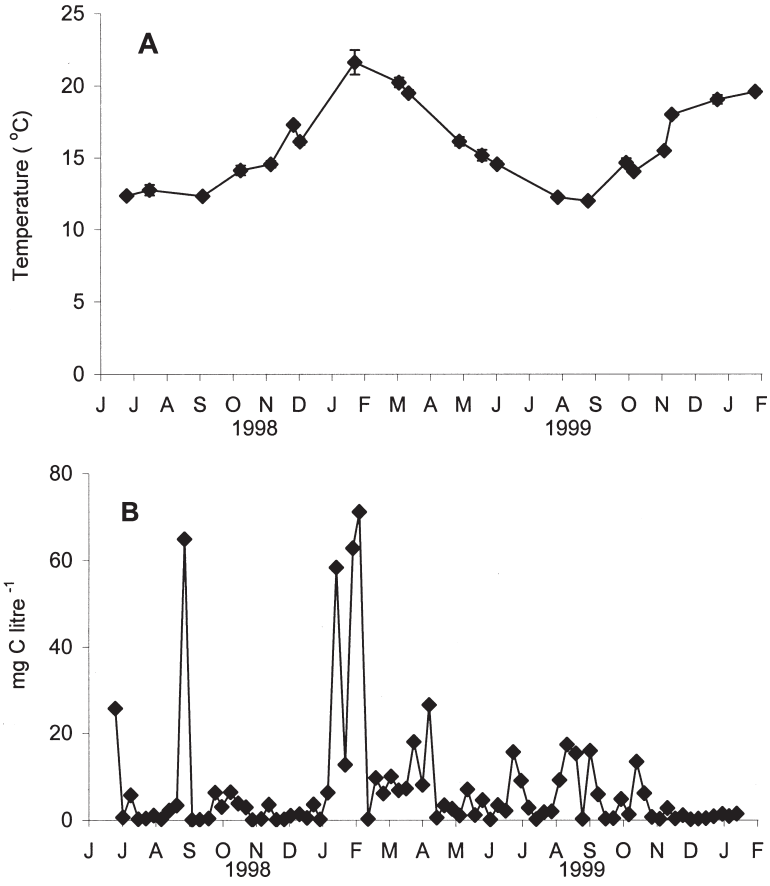

Fig. 1 Seasonal variations in: **A**, seawater temperature and; **B**, phytoplankton biomass, expressed as organic carbon (C) from the Marlborough Sounds, New Zealand, from June 1998 to January 2000.

gonad tissue entered a resting phase with gametogenesis resuming in August.

Dry weight relationships and reproductive output

From April 1998 to February 2000 the total dry weight of 110-mm-length oysters varied seasonally (Fig. 5) with minimum values in April 1988 and January 1999. The sample condition index ranged from 5.3 to 12.1 and followed the dry weight relationships. The somatic and reproductive tissue weight were positively correlated (Table 1), increasing over the winter. Maximal gonad dry weights (>3 g) were recorded in November and December 1999 when reproductive tissue comprised 65% of the total dry weight. The sharp decline in mean gonad dry weight in January 1999 and 2000 most likely reflected weight loss as a result of spawning.

The length dry weight relationships for *C. gigas* collected in December and January fitted the allometric function defined in Equation 1 (Fig. 6). The best-fit values of model parameters obtained were: $a = 4.22 \times 10^{-4}$ and $b = 3.74$ ($n = 56$, $R^2 = 0.94$) for oysters with mature gonad collected in December, and $a = 1.65 \times 10^{-3}$ and $b = 2.86$ ($n = 36$, $R^2 = 89$) for oysters collected in January.

The minimum length for spawning was c. 6 cm shell length for an individual with a dry tissue weight of 0.5 g. The reproductive output, represented by the difference in dry tissue weight between pre-spawned and post-spawned individuals, increased with shell length. For a 10-cm-shell oyster the gametes formed 48% of the dry tissue weight and for a 13-cm-length oyster this increased to 59%.

Biochemical composition

Seasonal variation occurred in the biochemical composition of the whole body tissues, proteins (40–63% dry weight), lipids (1–8%), and glycogen (2–8%). The biochemical composition of separated gonad and somatic tissues varied with season and

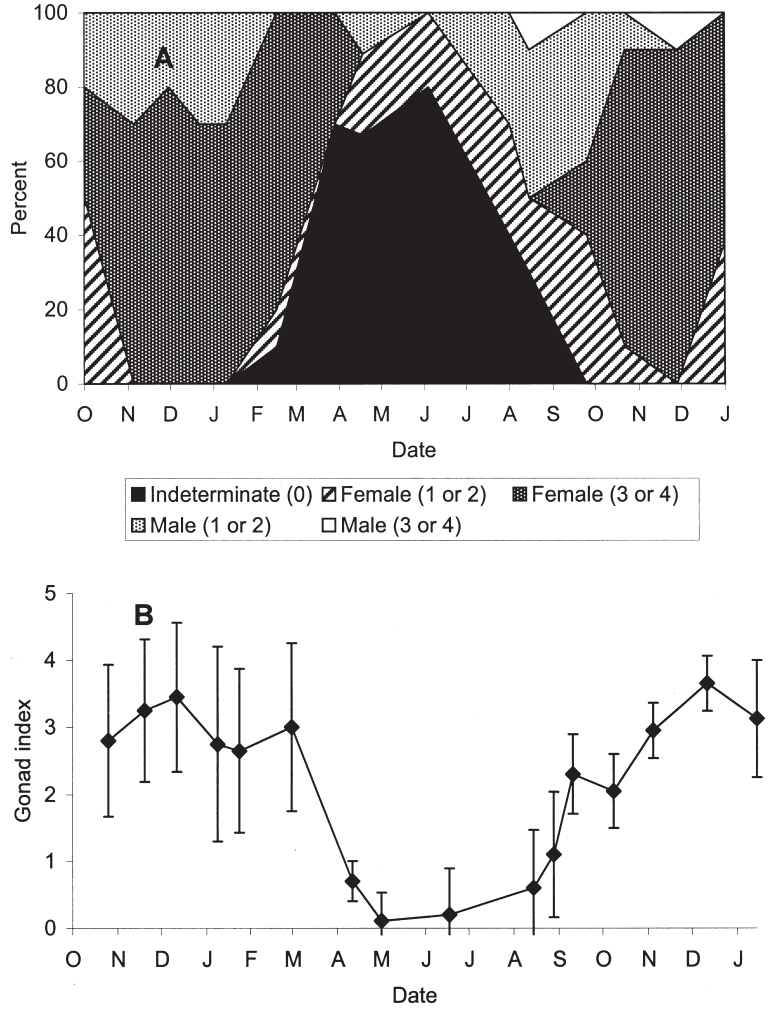

Fig. 2 Seasonal variations in oyster *Crassostrea gigas* gonad development, based on visual staging of histological sections, from July 1998 to January 2000. **A**, Percent of each gonad stage; and **B**, mean sample gonad index ± standard deviation.

between years (Fig. 7). Glycogen content varied between 1 and 8% dry weight of tissue and was similar in both somatic and reproductive tissues for the first part of the study (June 1998–March 1999). During the winter of 1999 glycogen values in the gonad tissue in the mantle were elevated compared with the other somatic tissue. During the final gamete maturation and spawning phases (November–February) the proportion of glycogen in the gonad tissue was below that in the somatic tissues.

Lipid content of the gonad was generally higher than the somatic tissue with peaks (up to 10% dry weight) during the winter and early summer. Higher values in August and April coincided with peaks in phytoplankton biomass. Lipid composition of the somatic tissue was consistently low (<4%) for the duration of the study and there was an inverse relationship between seawater temperature.

There was little seasonal variation in the protein content of the somatic tissue with an average of c. 50%. In contrast, for gonad protein there was a clear seasonal cycle in both years. Lowest protein content (<30%) occurred in winter (May–August) and values similar to the somatic tissues were found from November to March. Gonad protein correlated positively with both the seawater temperature and the gametogenic cycle (Table 1), increasing with both the population gonad index and oocyte diameter. There was also an inverse relationship between % protein and % glycogen in the oyster gonad.

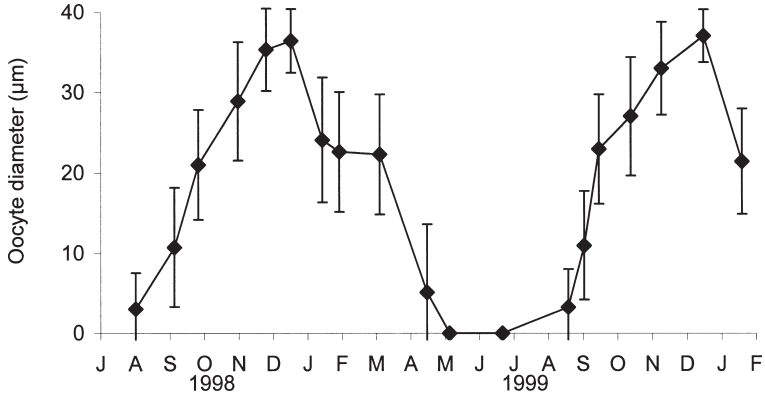

Fig. 3 Seasonal variation in mean oocyte diameter (± standard deviation) in *Crassostrea gigas* between August 1998 and January 2000.

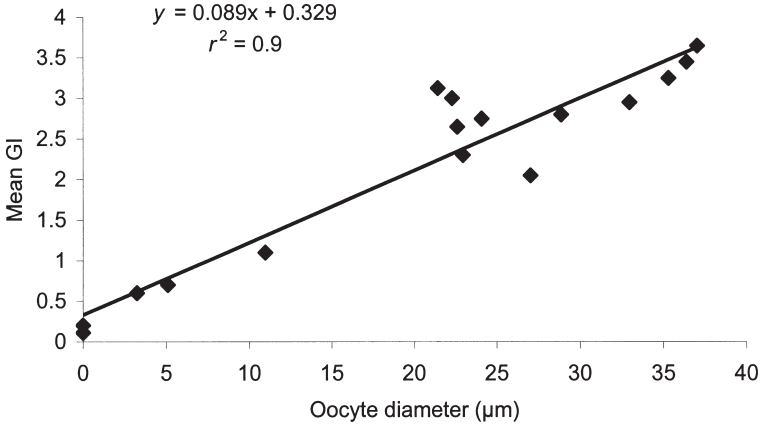

Fig. 4 Relationship between mean gonad index (GI) and mean oocyte diameter in *Crassostrea gigas* collected between November 1998 and January 2000.

Table 1 *Crassostrea gigas* correlation coefficients relating environmental variables, oyster weight relationships, and biochemical components. (PC, phytoplankton biomass (organic carbon); PN phytoplankton abundance; T, seawater temperature; OD, oocyte diameter; GI, sample gonad index; GW, dry weight of gonad; SW, somatic tissue dry weight; TW, total dry weight; CI, population condition index; GS, somatic tissue glycogen; GG, gonad glycogen; LS, somatic tissue lipid; LG, gonad lipid; PS, somatic tissue protein; PG, gonad protein. $N = 19$, critical values $P_{0.05} = 0.391$, $P_{0.01} = 0.535$.)

	PC	PN	T	OD	GI	GW	SW	TW	CI	GS	GG	LS	LG	PS	PG
PC	1	0.09	0.27	–0.06	0.00	–0.39	–0.43	–0.44	–0.39	–0.25	–0.15	–0.05	–0.10	0.14	0.12
PN		1	–0.03	–0.29	–0.24	–0.31	–0.11	–0.27	–0.31	0.01	0.01	0.01	0.01	0.04	–0.19
T			1	0.56	0.67	0.09	–0.35	–0.06	–0.23	–0.80	–0.77	–0.61	–0.30	0.29	0.80
OD				1	0.97	0.68	–0.05	0.48	0.53	–0.38	–0.71	–0.34	–0.40	0.27	0.90
GI					1	0.57	–0.17	0.36	0.41	–0.48	–0.79	–0.39	–0.44	0.26	0.94
GW						1	0.61	0.96	0.87	0.21	0.19	–0.35	–0.40	0.33	0.44
SW							1	0.82	0.53	0.67	0.52	–0.28	–0.24	0.24	–0.26
TW								1	0.83	0.40	0.06	–0.36	–0.38	0.33	0.23
CI									1	0.44	–0.03	–0.06	–0.23	0.13	0.20
GS										1	0.82	0.10	–0.10	0.02	–0.63
GG											1	0.21	–0.14	0.01	–0.84
LS												1	0.63	–0.56	–0.47
LG													1	–0.72	–0.40
PS														1	0.30
PG															1

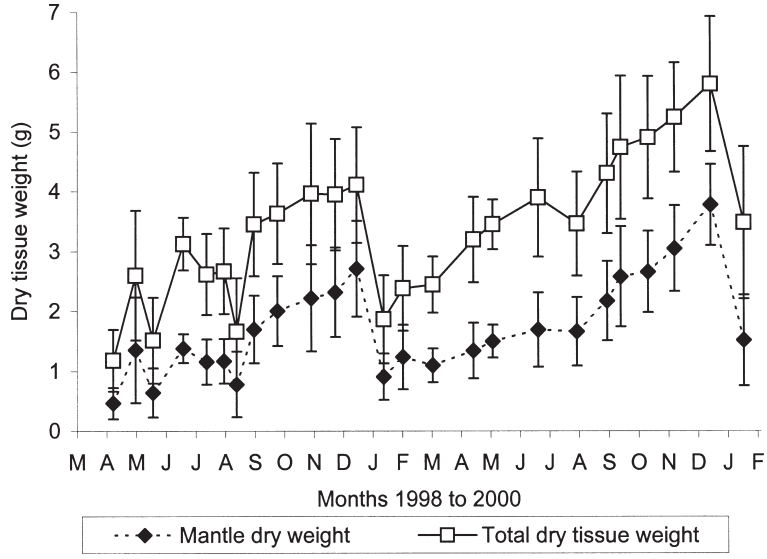

Fig. 5 Seasonal variation in mean total oyster tissue dry weight including gonad tissue from the mantle for oysters *Crassostrea gigas* collected from April 1998 to January 2000.

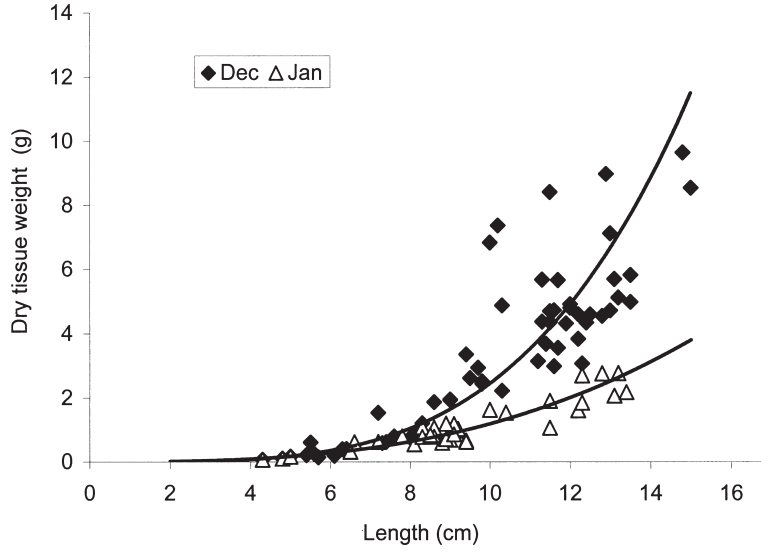

Fig. 6 Relationship between dry tissue weight and shell length for pre-spawned oysters, collected in December, and post-spawned oysters *Crassostrea gigas*, collected in January.

DISCUSSION

In Croiselles Harbour, Malborough Sounds, the Pacific oyster *C. gigas* has a regular seasonal cycle of gonad maturation which differs from that recorded from northern New Zealand (Dinamani 1987). In the present study, gametogenesis was reduced from April to August and increased rapidly in the spring reaching a maximum in December. A single spawning occurred over a short period and may have been restricted to December and January. This contrasts with a longer breeding cycle in northern New Zealand where there were two or more spawning periods with maximal spawning in February and March (Dinamani 1987).

Worldwide, the timing of the reproductive cycle of *C. gigas* from gametogenesis to spawning, is controlled by an interaction of environmental and endogenous factors (Sastry 1979). The differences in the timing of gonad development and spawning in oyster populations within New Zealand may be explained in part by lower seawater temperatures recorded from the South Island. Gametogenesis in *C. gigas* is temperature dependent (Shpigel 1989;

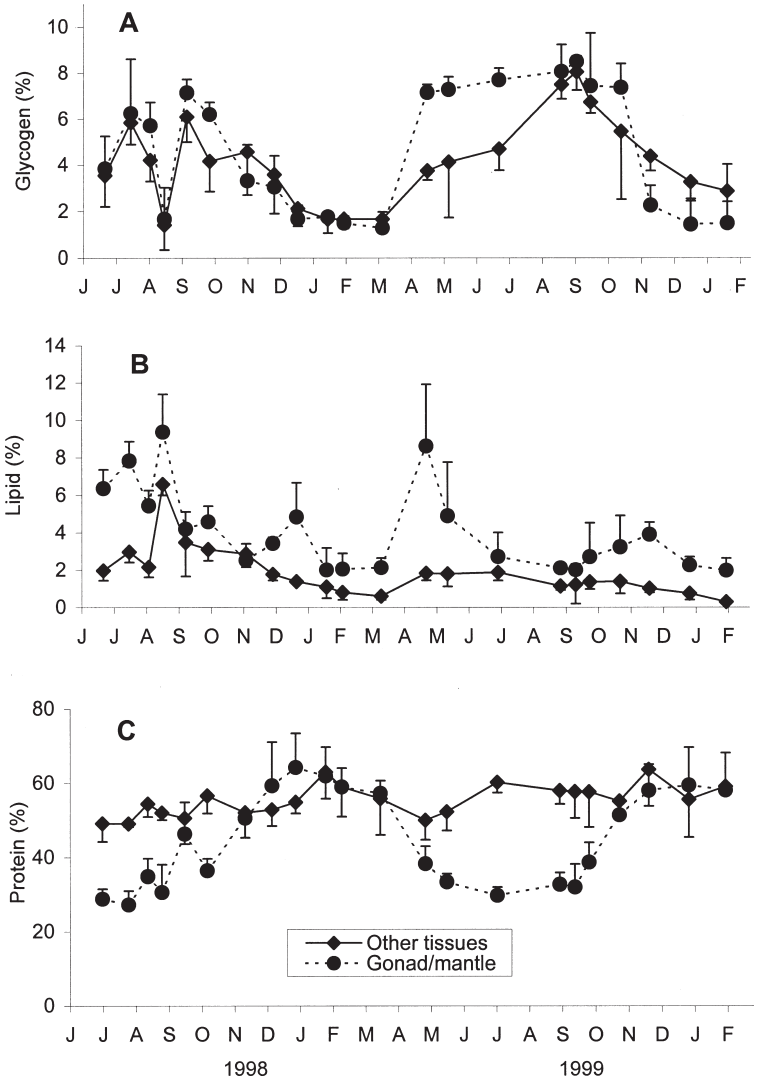

Fig. 7 Biochemical components of gonad from the mantle (dashed lines) and somatic tissue (solid lines) expressed as percentage of dry tissue weight (± standard deviation) of *Crassostrea gigas*, from June 1998 to January 2000. **A**, Glycogen; **B**, lipid; and **C**, protein.

Ruiz et al. 1992) and in Korea (Kang et al. 2000) begins in the autumn at temperatures close to 10°C. In the present study some early gametogenesis occurred during the autumn and winter at temperatures close to 12–13°C, but the majority of individuals were reproductively inactive. Maximal gonad maturity was in December and spawning most likely occurred, as in other studies, when minimum seawater temperatures exceeded 18°C (Mann 1979). Ruiz et al. (1992) found that small inter-annual and seasonal variations in the gonad cycle were temperature related. In the present study, temperature was also the main factor that correlated with the reproductive cycle.

Little oogenesis was recorded over winter for Marlborough oysters and early gametogenesis was characterised by an average oocyte diameter close to 10 µm in spring (August, September) and autumn. This is within the size range described by Lango-Reynoso et al. (2000) for *C. gigas* populations along the French Atlantic coastline. Also, oocyte size was similar between years (Lango-Reynoso et al. 2000). Oocytes that began gametogenesis in January do not mature fully and over winter the gonad material is most likely reabsorbed, stored, and recycled to satisfy basal metabolism. The maximal oocyte growth phase was characterised at oocyte diameters close to 20 µm and the mature ova stage at c. 35 µm.

Very few individuals were in the degenerating phase (46 µm) which suggests that spawning may not have occurred. Pacific oysters from some locations may undergo gametogenesis but do not spawn. This has been linked to a failure to meet a minimum temperature (Mann 1979; Ruiz et al. 1992) or unfavourable environmental conditions (Steele & Mulcahy 1999).

In oysters the rate of gametogenesis is thought to be dependent on temperature intensity and time, stored reserves, and food availability (Mann 1979; Sastry 1979; Muranka & Lannan 1984; Wilson & Simons 1985; Shpigel 1989). In the present study, temperature appeared to be the major factor affecting the reproductive cycle. In some species, gonad growth has been associated with food availability with chlorophyll *a* concentrations explaining differences in oyster gonad proliferation and spawning intensity in populations in Spain, Portugal, and Korea (Ruiz et al. 1992; Almeida et al. 1997; Kang et al. 2000). Chlorophyll *a* measurements were not available as part of our study and algal biomass did not correlate directly with the gonad index or oocyte diameter. However, during the first year of the study, when the phytoplankton biomass was low, oyster dry weight remained low throughout the winter. During the following year, with increased phytoplankton biomass, there was consistent weight increase throughout the winter and rapid growth in the spring. These results suggest that nutrient accumulation over winter is as important in the growth of oysters as in other bivalves (Bayne 1976; Heffernan et al. 1989; Harvey et al. 1993; Honkoop & van der Meer 1997; Beukema et al. 2001). As in most bivalves, the reproductive potential of Marlborough Pacific oysters increased with shell length (Brown & Russell-Hunter 1978) and weight loss occurred as a result of spawning (Dame 1976; Griffiths & King 1979; Griffiths 1981; Thompson 1984). For Marlborough oysters the reproductive tissue made up 65% of the total dry tissue weight and gamete production was similar to that found for several cohorts of Pacific oysters from Spain (Cigarria 1999).

Biochemical changes within New Zealand oyster tissues were associated with the reproductive cycle as described from the histological examinations and the weight relationships (Mann 1979; Kang et al. 2000). Because most studies have calculated biochemical components for the total body tissues they do not consider the transfer of materials between different body tissues. In their study Berthelin et al. (2000a) measured the biochemical composition of different tissues including the adductor muscles, gonad/mantle and digestive gland. They concluded that proteins from muscle tissue contributed little to the reproductive tissue which forms from glycogen and lipids stored in the digestive gland, mantle, and gonad. These changes are consistent with the biochemical composition of the reproductive and somatic tissues investigated in the present study. Patterns of somatic growth were reflected in the protein concentrations that were maintained above 50% throughout the year with little seasonal or inter-annual variation. This suggests that somatic tissue growth occurs over the winter and continues during gametogenesis. This contrasts with some bivalve species where somatic and shell growth is inhibited during gametogenesis and spawning (Harvey et al. 1993; McLachlan et al. 1996).

As expected, the % protein in the gonad tissues reached a maximum in December and a minimum in June, correlating with the seawater temperature. The values (30–65%) were similar to those found in the digestive gland of oysters from France (Berthelin et al. 2000a). The protein content increased with gonad dry weight, the population gonad index, and oocyte diameter. This latter relationship was also recorded in ovarian tissues by Li et al. (2000) working on Pacific oysters from Spain. In the present study, minimum protein values in the gonad region of the mantle were close to 30% in the winter, suggesting that at low temperatures, protein may be utilised for both metabolic energy and somatic growth.

Glycogen and lipid proportions in oyster tissues varied considerably seasonally and between years within the range <2–12%. Where comparisons can be made the total body lipids are within the range recorded for Pacific oysters from other parts of the world (Mann 1979; Pazos et al. 1996; Almeida et al. 1997; Kang et al. 2000). However, the total lipid in the gonad tissue is low compared with oysters from Spain and France (Ruiz 1992; Li et al. 2000) at seawater temperatures similar to New Zealand. These differences with location may reflect either food quantity or quality, in particular the proportion of triacylglycerols in the diet (Pazos et al. 1996). Although the % lipid in the present study showed no consistent pattern seasonally, values were higher in the gonad tissue than the remaining somatic tissue. There were peaks in lipid concentrations in autumn and winter that corresponded with phytoplankton blooms and lipid concentrations increased during gametogenesis and fell during spawning. Interestingly, in this and other studies, there was an

inverse relationship between temperature and the amount of fatty acids in the tissues of oysters (Chu & Greaves 1991; Pazos et al. 1996). In the present study the lipid reserves in the gonad portion of the mantle fell over the winter of 1999 suggesting that they may have been mobilised to provide energy as the carbohydrate reserves become depleted (Bayne 1976; Barber & Blake 1981).

Carbohydrates are recognised as the major energy source in bivalves (Gabbott 1975) and the seasonal changes in glycogen levels of somatic and reproductive tissues of Marlborough oysters correlated with seawater temperature, condition, and tissue dry weight. There were differences in the glycogen content in the 2 years of study, in particular low glycogen values late in the winter (August) of 1998 when the phytoplankton densities were low. Other periods of low glycogen occurred during the reproductive cycle when pre-stored glycogen is converted into lipid during vitellogenesis. There was high glycogen in the mantle tissues between April and August, before an increase in gonad volume (Perdue & Erickson 1984). At this time, when the gonad tubules are reduced, the mantle tissue contains numerous storage cells and there is maximal glycogen metabolism and storage capacity (Berthelin et al. 2000b).

In conclusion, the biochemical composition of Pacific oysters in the Marlborough region of New Zealand follow cycles of somatic growth and reproduction. The timing of the cycle and the amplitude of the cycles is correlated with seawater temperature and annual variations may depend upon the quality and quantity of the food supply. Oyster growth and gamete proliferation are likely to occur annually but gamete release may not occur unless appropriate environmental cues are present. For New Zealand oysters, these spawning cues are unknown but may include a minimum temperature, changes in salinity, photoperiod, and/or phytoplankton blooms. To assess the future aquaculture potential of the region further research is needed to determine the seasonal abundance of the larvae, their health—determined by their biochemical composition—and their settlement success.

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